Seasonal trends of Amazonian rainforest phenology, net primary productivity, and carbon allocation.

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Key Points

- Field data confirm Amazon forests maximise leaf production during dry season.
- Trade-offs in carbon allocation determine seasonality of *NPP* components.
- Consistent reproductive seasonality across contrasting precipitation regimes.

Abstract

The seasonality of solar irradiance and precipitation may regulate seasonal variations in tropical forests carbon cycling. Controversy remains over their importance as drivers of seasonal dynamics of net primary productivity in tropical forests. We use ground data from nine lowland Amazonian forest plots collected over three years to quantify the monthly *NPP* of leaves, reproductive material, woody material, and fine roots over an annual cycle. We distinguish between forests that do not experience substantial seasonal moisture stress ("humid sites") and forests that experience a stronger dry season ("dry sites"). We find that forests from both precipitation regimes maximise leaf *NPP* over the drier season, with a peak in production in August at both humid (mean 0.39 ± 0.03 Mg C ha^{-1} mo^{-1} in July, n = 4) and dry sites (mean 0.49 ±0.03 Mg C ha^{-1} mo^{-1} in September, n = 8). We identify two distinct seasonal carbon allocation patterns (the allocation of *NPP* to a specific organ such as wood leaves or fine roots divided by total *NPP*). The forests monitored in the present study show evidence of either: (i) constant allocation to roots and a seasonal trade-off between leaf and woody material; or (ii) constant allocation to wood and a seasonal trade-off between roots and leaves. Finally, we find strong evidence of synchronised flowering at the end of the dry season in both precipitation regimes. Flower production reaches a maximum of 0.047 ±

0.013 and 0.031 ± 0.004 Mg C ha^{-1} mo^{-1} in November, in humid and dry sites respectively. Fruitfall production was staggered throughout the year, probably reflecting the high variation in varying times to development and loss of fruit amongst species.

Keywords: Net primary productivity, daily insolation, precipitation, seasonality, phenology, canopy, leaf, flower, fruit, wood, roots.

1. Introduction

Controversy remains over the roles of solar irradiance and precipitation as the main drivers of seasonal dynamics of the net primary productivity (*NPP*) of tropical forests. Whereas a relationship between seasonal peaks in precipitation and wood productivity is relatively well established for Amazonian forests [*Brienen and Zuidema,* 2005; *Rowland et al.,* 2013; *Wagner et al.,* 2012; *Hofhansel et al.,* 2015], the predominant drivers of the seasonal production of leaf and reproductive organs remain unclear. Systematic ground-based monitoring of the major components of biomass productivity is needed to understand the trends governing their seasonality.

Apparent seasonality of leaf phenology has been observed from optical remote sensing data [*Huete*, 2006, *Myreni*, 2007, *Saleska*, 2007, *Brando*, 2010, *Wu et al.*, 2016] and, to a lesser extent, from ground-based collection of leaf litter from litterfall traps [*Chave et al.,* 2010]. The former produced divergent results and has generated controversies around the validity and interpretation of seasonal variation in remotely sensed metrics in moist tropical forests, leading to ongoing controversy over the proposed paradigm of light-limited forests responding to a surge of solar irradiance during the dry season [*Morton et al.,* 2014]. Litterfall studies provide evidence of

positive correlations between litterfall and rainfall seasonality, but it remains unclear how timing of leaf litterfall is related to the timing of canopy leaf production.

Much of the literature and debate on the seasonality of Amazon canopy leaf production has implicitly assumed a positive relationship between canopy "greening" and overall ecosystem productivity. However, a question that remains unresolved is the extent to which a seasonal increase in canopy leaf production reflects an increase in overall productivity, or alternatively simply a shift in carbon allocation among roots, wood, the canopy, and non-structural carbohydrate storage pools. A recent study in Bolivia has demonstrated that allocation shifts are more important than overall changes in productivity in explaining interannual variability in canopy, wood and fine root growth rates [*Doughty et al.* 2014a]. Here, we investigate the physical drivers of carbon allocation across a wider range of Amazonian sites, test if Amazon rainforests may be separated into radiation-controlled and precipitation-controlled forests, and explore the arguments from an evolutionary perspective.

A third set of relevant questions revolve around the nature and timing of reproductive phenology in tropical forests, how this relates to the overall seasonality of climate and productivity, and the amount of productivity invested in reproduction. The links between flowering phenology, weather parameters (solar irradiance, rainfall, temperature), and an the potential role of an intrinsic biological clock developed as an evolutionary response to biotic interactions (pollination, seed dispersal) remain to be deciphered [*Lieberman,* 1982; *Wright and van Schaik,* 1994; *Wright and Calderon,* 1995; *Leigh,* 1999; *Brochert et al.*, 2002, 2005; *Calle et al.*, 2010; *Pau et al.*, 2013].

All these interlinked questions can potentially be examined by a multi-year dataset comprising measurements of all the major components of forest *NPP* at seasonal resolution, and across contrasting sites in Amazonia. Here we present such a dataset as a contribution to this debate, presenting data over three years from a network of one hectare permanent plots: the Global

Ecosystems Monitoring network (GEM, gem.tropicalforests.ox.ac.uk). Our analysis is focused on nine plots located in old growth intact Amazonian forests (Table 1). Forest plots were categorised into two precipitation regimes: sites that did not experience a strong dry season (termed "humid sites" for the purpose of this paper), and those that experienced a dry season over several months (termed "dry sites").

In this study, we ask the following questions:

(1) Is there field-based evidence of a peak in the net primary productivity of leaves (NPP_{Leaves}) during the dry season, as suggested by existing optical remote sensing observations?

(2) How does the net primary productivity of flowers ($NPP_{Flowers}$), fruit (NPP_{Fruit}), above-ground coarse woody material (NPP_{ACW}), and fine roots ($NPP_{Fine\ roots}$) vary over the seasonal cycle in humid and dry sites?

(3) Is there evidence of clear trade-offs in carbon allocation driving seasonal variation of woody growth, canopy production and fine root production? If so, how do these trends vary across sites?

2. Methods

2.1. Site description

Our study region is across the Amazon forest biome. Nine 1 ha long term intensive carbon monitoring plots were established in lowland Amazonia as part of the Global Ecosystems Monitoring Network (GEM) of intensive plots, and nested with the RAINFOR Amazon Forest Inventory network (RAINFOR) of 1 ha plots. Two plots were in the Tambopata reserve,

Tambopata Province, Department of Madre de Dios, Peru (RAINFOR codes TAM-05, TAM-06); two plots in the province of Maynas, on the Allpahuayo-Mishana National Reserve (ALP-01, ALP-30); two plots on private property at the Hacienda Kenia in Guarayos Province, Santa Cruz, Bolivia (KEN-01, KEN-02); two plots in the Fazenda Tanguro, Mato Grosso State, Brazil (TAN-05, TAN-06); and three plots in Caxiuanã National Forest Reserve, Pará in the eastern Brazilian Amazon (CAX-03, CAX-06, CAX-08). Several plots have been established for over eight years. However, we chose to include data collected over the period 2009 - 2012 for this analysis, to ensure the same data collection period between plots. All plots were selected in areas with relatively homogeneous stand structure. All had closed canopies without any large gaps. Forest composition varied across the sites, both across the region and between neighbouring plots because of edaphic or disturbance history factors.

Site classification - Sites were classified into dry and humid sites, according to estimates of maximum climatological water deficit (MCWD), and following the classification described in *Malhi et al.* [2015]. Our classification differs from that of *Doughty et al.* [2015] in one way: whereas *Doughty et al.* [2015] classify KEN-01 as wet forest, based on species composition (Amazonian tree species vs Chiquitano dry forest species) and edaphic characteristics (deep vs shallow soils), we classify this site as dry forest, based on mean MCWD, as Kenia is on the extremely dry end of the climate spectrum of Amazonia. Both plots in the Kenia site experience identical climate and are 1 km apart – the difference in species composition is driven by soil depth affecting dry season water supply. The distinction into humid and dry sites made by *Doughty et al.* [2015] was relevant in the context of a study on drought effects. In our context of exploring seasonal variation of NPP, both Kenia plots experience an extreme dry season and should be classified together,

2.2. Weather

Time series for solar irradiance (W m^{-2}), air temperature (˚C), relative humidity (%) and precipitation (mm mo^{-1}) were collected from an Automatic Weather Stations (AWS, Campbell Scientific) located ca. 1 km from each experimental site. These data were quality controlled to remove outliers, and monthly time series were gap-filled as described in *da Costa et al.* [2014], *Doughty et al.* [2014c], *Malhi et al.* [2014], *del Aguila-Pasquel et al.* [2014], and *Araujo-Murakami et al.* [2014].

2.3. Net primary productivity

All sites were monitored according to the Global Ecosystems Monitoring (GEM) network protocol. Methods are described in detail in the field manual available on the website: http://gem.tropicalforests.ox.ac.uk, as well as in a series of site-specific papers. *da Costa et al.* [2014], *Doughty et al.* [2014c], *Malhi et al.* [2014], *del Aguila-Pasquel et al.* [2014], and *Araujo-Murakami et al.* [2014] provided comprehensive site descriptions and the complete carbon cycles for these sites (Table 1) [*Malhi et al.* 2015]. The protocol measures and sums all major components of *NPP* and *R*a on monthly timescales in each 1 ha forest plot. The present paper focuses on the *NPP* components of these measurements. Recognizing that many of these measurements have potential systematic uncertainties, we assigned sampling or systematic uncertainties in our calculations of total *NPP*, *R*a, *GPP* and *CUE*. Each measurement presented in the present paper has a rigorous error propagation presented in the series of site-specific papers cited above.

The GEM methodology has shown close agreement with independent eddy covariance data on annual timescales for both *R*a and *GPP* [*Malhi et al.* 2009, *Fenn et al.* 2014]. The following paragraphs provide a brief description of the field methods used in the present study. We briefly discuss the potential biases accrued by each measurement.

Above-ground coarse woody net primary productivity - We determined plot-level NPP_{ACW} using multiple censuses (2009, 2010, 2011) of the forest plots and three-monthly dendrometer band measurements (2009 - 2011). We completed tree censuses to determine the growth rate of existing surviving trees and the rate of recruitment of new trees. Data on diameter at breast height (dbh, using diameter tape) and tree height (using clinometer when possible, or a visual estimate) were recorded for all trees ≥ 10 cm dbh. Above-ground coarse woody biomass was calculated using the allometric equation of *Chave et al.* [2005] for tropical moist forests, employing data on diameter, height and wood density.

$$AGB = 0.0509 \times (\rho \times dbh \times H) \quad (1)$$

where AGB is above-ground biomass (kg), ρ is density of wood (g cm^{-3}), dbh is diameter at breast height (cm), and H is height (m). Wood density was estimated for each species from a global database of tropical forest wood density [*Chave et al.*, 2009; *Zanne et al.*, 2009], ideally assigned to species, but to genus or family level where species identity or species-level wood-density data were not available. To convert biomass values into carbon, we assumed that dry ACW biomass is 47.3% carbon, based on recent studies in lowland forests in Panama that included volatile carbon compounds not recorded by conventional dry assessment [*Martin and Thomas*, 2011]. For the few trees where height data were not available we estimated height by employing a plot-specific polynomial regression between dbh and height [*Feldspauch et al*., 2011]. Annual NPP_{ACW} was calculated as the sum of biomass increase of individual surviving trees between census intervals.

To determine seasonal variation in woody growth rates, we installed dendrometer bands in 2009 on approximately 200 randomly selected trees in each plot (all trees in TAM-05 and TAM-06). The dendrometer bands were measured every three months with callipers. The dendrometer data were scaled up to 1 ha by using the annual full census data to determine the ratio of wood net primary productivity (NPP_{ACW}) of all trees over the NPP_{ACW} of dendrometer trees. This ratio provided a scaling factor that we applied to the dendrometer data, to estimate seasonal NPP_{ACW} for the entire plot (i.e. to include trees that had no dendrometers), with the implicit assumption that the productivity of the dendrometer trees is representative of the wider population.

One concern is the effect of seasonal changes in hydraulics, the possible bias introduced by moisture expansion and shrinkage of the bark or xylem on tree growth seasonality. To estimate the effect of moisture expansion on apparent tree growth during the wet season, *Doughty et al.* [2015] separated the trees with almost no annual tree growth (woody *NPP* <1 kg C ha^{-1} $year^{-1}$) and quantified their apparent seasonal trends in diameter. For these slow or non-growing trees, we found a mean seasonal amplitude of apparent growth peaking in April and decreasing until October. For example, for our two Bolivian sites we estimated the seasonal effect of moisture expansion between March and November (the maximum and minimum) to be an apparent change of 0.08 Mg C ha^{-1} $month^{-1}$ and 0.19 Mg C ha^{-1} $month^{-1}$, although this may underestimate the effect, since faster growing trees tend to shrink more in the dry season, because they possess larger vessels [*Rowland et al.*, 2014]. As the census interval was small (1 year) we did not apply a correction for trees that grow and die between census intervals without being recorded [*Malhi et al.*, 2004]. We did not account for the wood productivity of lianas, although their leaf productivity is recorded by litterfall traps.

Litterfall - Canopy litterfall was collected in 25 0.25-m^2 (50 × 50 cm) litter traps installed 1 m above the ground on each plot. Litterfall was collected every 15 days over a period of 18 or 24 months between 2009 and 2011, split into different components (leaves, fruits, flowers, seeds, woody tissue, bromeliads, other epiphytes -non-vascular epiphytes, mosses, liverworts-, and unidentified fine debris), oven dried at 80ºC, and weighed. Annual estimates of leaf loss to herbivory were obtained from scans of litterfall, according to *Metcalfe et al.* [2013]. Seasonal variation of large palm leaf litter was not accounted for in the lowland plots, implying an underestimation of litterfall at the TAM-06 site in particular (*Malhi et al.* [2014])

There are two potential seasonal biases in litterfall. First, decomposition of litter may increase during the wet season; this would imply that our measurements underestimate wet season litterfall, although collecting litterfall every 15 days ensures minimum loss by decomposition. Second, we do not correct litterfall data to account for seasonal leaf herbivory. On an annual timescale, *Metcalfe et al.* [2013] estimated an average canopy loss of 7% ± 0.5% in nine Andean and Amazonian plots, including Tambopata. Although we did not find clear seasonal trends for herbivory in our lowland Amazonian sites, *Lieberman* [1982], *Aide* [1988], and *Givnish et al.* [1999] estimated that insect activity increases in the wet season.

Canopy productivity – Canopy litterfall is a good estimator of canopy productivity on annual or larger timescales. However, it represents the timing of canopy biomass loss, not biomass gain, and hence cannot record seasonal variation in canopy productivity. To overcome this issue, we combined data sets of canopy litterfall, canopy Leaf Area Index (LAI) [*da Costa et al.*, 2014; *Doughty et al.*, 2014c; *Malhi et al.*, 2014; *del Aguila-Pasquel et al.*, 2014; *Araujo-Murakami et al.*,

2014], and Specific Leaf Area (SLA) [*Salinas et al.*, 2011] to estimate the seasonal cycle of canopy net primary productivity (NPP_{Canopy}) in each plot [*Doughty and Goulden*, 2008]:

$$NPP_{Canopy} = (\Delta LAI / SLA) + litterfall \quad (2)$$

where ΔLAI is the change in LAI between months ($m^2\ m^{-2}$), SLA is the mean specific leaf area ($m^2\ g^{-1}$), and litterfall is total litterfall ($g\ m^{-2}$). We assume no difference in SLA in between mature and senescent leaves, and do not attempt to account for resorption of carbon in senescent leaves. Both these uncertainties are likely to be small.

We estimated LAI using canopy images recorded with a digital camera and hemispherical lens and analysed with CAN-EYE software (http://www6.paca.inra.fr/can-eye). We estimate SLA by taking a subsample of fresh leaf litterfall, scanning each leaf to determine fresh leaf area, and then drying at 80°C and weighing the leaf to determine dry mass. SLA is fresh leaf area divided by dry leaf mass. Leaf area was calculated using image analysis software, Image J freeware (http://rsb.info.nih.gov/ij/). NPP_{Canopy} is estimated in $g\ m^{-2}$. This method is purely based on a mass balance approach. We are providing estimates of changing stocks of litterfall over time, without making assumptions on leaf age.

Fine root productivity – We collected fine roots (< 5 mm diameter) from sixteen ingrowth cores (12 cm diameter, 30 cm depth) every three months from September 2009 to March 2011. Roots were manually removed from the ingrowth cores in four 10 min time steps and the trend of cumulative extraction over time vas used to predict root extraction beyond 40 min, as described in *Metcalfe et al.* [2006]. Root-free soil was then replaced in each ingrowth core, keeping the same bulk density of the undisturbed soil. Collected roots were thoroughly rinsed, oven dried at 80˚C to

constant mass, and weighed. Monthly $NPP_{\text{Fine roots}}$ was estimated from the quantity of fine root mass produced in the three month interval since the last collection, allowing us to estimate seasonal fine root growth. While most ecological studies define fine roots as < 2 mm, we noted that a few roots between 2 and 5 mm also grow into our ingrowth cores. For pragmatic reasons we did not separate these out; these may account for a few percent of root biomass in our ingrowth cores. This definition of fine roots also maintains consistency with our other recent papers [*Doughty et al.* 2014a, *Malhi et al.* 2015, *Doughty et al.* 2015].

As in all carbon budget measurement protocols, the measurement of roots proved to be the most challenging. We report results from ingrowth cores as they have previously provided robust estimates of root productivity over seasonal and annual timescales. For example, *Girardin et al.* [2013] provide detailed comparisons and show excellent agreement of results obtained from ingrowth cores and rhizotrons in six GEM plots located in Andean and Amazonian forests, including the Tambopata plots presented here.

Total net primary productivity. – *NPP* can be estimated as the sum of NPP_{ACW}, NPP_{Canopy}, branch turnover ($NPP_{\text{BranchTurnover}}$), $NPP_{\text{Fine roots}}$, coarse roots ($NPP_{\text{Coarse roots}}$) and volatile organic compound production (NPP_{VOC}).

$$NPP_{\text{AG}} = NPP_{\text{ACW}} + NPP_{\text{Canopy}} + NPP_{\text{BranchTurnover}} + NPP_{\text{Fine roots}} + NPP_{\text{CoarseRoots}} + NPP_{\text{VOC}} \quad (3)$$

We obtained seasonal NPP_{ACW} estimates from the dendrometer band growth, and NPP_{Canopy} values through the seasonal litterfall measurements coupled with seasonal variation in Leaf Area Index. Branch turnover and coarse root productivity are difficult to estimate at seasonal resolution [*da Costa et al.*, 2014*; Doughty et al.*, 2014c*; Malhi et al.*, 2014*; del Aguila-Pasquel et al.*, 2014*; Araujo-Murakami et al.*, 2014] hence for the purpose of this paper, we concentrate on NPP_{ACW},

NPP_{Canopy} and $NPP_{Fine\ roots}$ seasonality. Finally, we did not estimate the contribution of volatile organic carbon emission from vegetation, which was found to be a very minor contribution in lowland tropical forest ecosystems [*Malhi et al.*, 2009].

The GEM protocol methodologies are used by many research groups globally, and in numerous published scientific studies. Each measurement incorporated in this paper is presented in detail in a series of five companion papers [*da Costa et al.*, 2014; *Doughty et al.*, 2014c; *Malhi et al.*, 2014; *del Aguila-Pasquel et al.*, 2014; *Araujo-Murakami et al.*, 2014].

Our estimates of total *NPP* is based on the summation of independent measurements (litterfall, tree growth, fine root production and branch fall). While some of these terms can carry substantial measurement and scaling uncertainties, the sampling uncertainties are independent for each measurement. Hence, some of these uncertainties potentially cancel each other out, reducing the overall uncertainty of the *NPP*, *GPP* and *CUE* estimates obtained using the GEM protocol. By contrast, an eddy covariance-based estimate of *GPP* is based on a single type of measurement (of net ecosystem exchange); hence any uncertainties in the method, such as underestimation of night-time respiration in stable atmospheric conditions, can result in an equivalent uncertainty in the final estimate of *GPP*. Malhi *et al.* [2015] and Doughty *et al.* [2015] explore the measurement and scaling uncertainties associated with each measurement taken by the GEM carbon budget and argue that a carbon summation measurement comprised of multiple independent measurements may be more accurate and less error prone than an eddy covariance-based estimate comprised of one type of measurement. One key difference between a top down (eddy covariance) and bottom up (GEM summation method) approach is that the latter gives an estimate on an annual and seasonal scale, whilst the former provide insight at the hourly (or less) scale.

The only uncertainties we considered for NPP values are those associated with sampling. We do not attempt to estimate systematic uncertainties, but note that in the context of this paper the key systematic biases of concern to us would be those which show a strong seasonal variation.

Analytical techniques - We used these data to describe the seasonal variation of NPP_{Canopy}, NPP_{ACW} and $NPP_{Fine\ roots}$. All uncertainty estimates are given as standard deviation (± SD). The propagated uncertainty for each variable described in the GEM protocol, including *NPP*, gross primary productivity (*GPP*), and carbon use efficiency (*CUE*), are provided in the five companion papers cited above. In the present paper, we focus on inter-annual (temporal) and inter-plot (i.e. spatial) variability of each *NPP* component. To estimate inter-annual variation, we estimate the inter-annual variation over three or (for Tambopata) four years for each plot, and provide the average of these variations for all plots: this is the typical inter-annual variation of a humid or dry plot. We estimate inter-site variation by calculating the SD of each *NPP* component for aggregated humid or dry plots. All temporal variability is presented as grey ribbons and the variability across plots is presented as error bars centred on the mean.

Ternary diagrams were used to explore trends in allocation of productivity over seasonal cycles in humid and dry forest sites. We explore the seasonal variance in allocation to each component using a ternary diagram of the variance of *NPP* allocation. A normalised allocation variance parameter, NVar(x) was calculated as:

$$NVar(x) = var(x) / (var(x) + var(y) + var(z)) \quad (4)$$

Where *var*(x) is the variance of the allocation coefficient of a variable *x*, and *y* and *z* are the other two allocation terms..

We explored the seasonal amplitude of each abiotic and biotic parameter. Seasonal amplitude was estimated by subtracting the minimum 3 months moving average from the maximum moving average recorded. Repeated-measures ANOVA was used to assess the significance of seasonal increases in productivity. All statistical analyses were performed with the R version 2.9.0 statistical package [Chambers, 2008]. The R scripts used to analyse the data are available on github.com/oxfordecosystemslab. As we are continually improving these scripts, the values we present may differ slightly between companion papers. All changes in the code since May 2014 are available online.

3. Results

3.1. Seasonal trends in weather

3.1.1. Solar irradiance

At all sites, solar irradiance increased towards the end of the dry season, reaching a peak during the dry to wet transition season, between August and October (Figure 1a). In most sites, light availability was above 150 W m^{-2} throughout the year. Allpahuayo, the cloudiest and wettest site, in NE Amazonia, experienced a more pronounced seasonality of solar irradiance, with values only increasing above 150 W m^{-2} between August and December (Figure 1a).

3.1.2. Precipitation

Mean monthly rainfall over the study period showed consistent seasonal trends at all sites, peaking between December and March. The dry season is defined as the period when potential evapotranspiration exceeds rainfall, typically when rainfall reaches values below 100 mm mo^{-1}. Humid sites do not experience a prolonged or intense dry season. The monthly precipitation of Allpahuayo exceeds 100 mm mo^{-1} throughout the year. Caxiuanã in NE Amazonia experiences a

long but mild dry season from August to November, when precipitation averages 59 mm mo^{-1}. On average, dry sites experience a significant ($t = 5.73$, $df = 4$, p-value < 0.0005) prolonged dry season from May to September (Figure 1b), although Caxiuanã experiences a dry season later in the year, from June to November (sup. mat. Figure S1).

3.1.3. Relative humidity

The seasonal amplitude of mean monthly relative humidity over the study period was strongest in Tanguro and Kenia in the southern limit of Amazonia. All other sites experienced little (Tambopata) to no (Allpahuayo, Caxiuanã) seasonal variation in relative humidity (Figure 1d).

3.1.4 Air temperature

Mean monthly temperature over the study period showed no consistent seasonal trends across the precipitation gradient (Figure 1c).

3.2. Seasonal trends in net primary productivity

3.2.1. Canopy productivity

The mean annual value for canopy Net Primary Productivity (NPP_{Canopy}) is 3.89 ± 0.10 Mg C ha^{-1} yr^{-1} (n = 8) for humid sites, and 4.50 ± 0.12 Mg C ha^{-1} yr^{-1} (n = 4) for dry sites. Total litterfall includes all canopy components, as described above.

There is a consistent surge in NPP_{Canopy} during the dry season in both precipitation regimes. NPP_{Canopy} reaches a maximum at the start of the dry season (May) in dry sites and at the height of the dry season (August) in humid and dry sites. The seasonal increase in NPP_{Canopy} is significant in

both humid (p-value < 0.005) and dry (p-value < 0.0005) sites. Mean monthly values over the study period range from 0.48 ± 0.17 Mg C ha^{-1} mo^{-1} to 0.20 ± 0.07 Mg C ha^{-1} mo^{-1} in humid sites and from 0.56 ± 0.23 Mg C ha^{-1} mo^{-1} to 0.22 ± 0.05 Mg C ha^{-1} mo^{-1} in dry sites (Figure 3b).

Canopy litterfall is produced throughout the year and increases at the onset of the dry season (August), coinciding with the peak in NPP_{Canopy}. Seasonality in LAI was not detected in these sites (not shown). LAI above or close to 5 will have some degree of saturation in both LAI 2000 and the photos, thus it is possible that we are not able to detect the seasonal trends in LAI in the less seasonal forests. As canopy production, which comprises (leaf, flower, fruit, twig, and unidentified material) is dominated by leaf productivity, we assume that the seasonal trends of canopy productivity are also those of leaf productivity.

3.2.2. Flower and fruit productivity

Flower - Annual estimates of flower net primary productivity (NPP_{Flower}) show no significant differences between humid and dry sites (p-value > 0.5). The mean annual value for NPP_{Flower} is 0.14 ± 0.01 Mg C ha^{-1} yr^{-1} (n = 8) for humid sites, and 0.09 ± 0.007 Mg C ha^{-1} yr^{-1} (n = 4) for dry sites.

NPP_{Flower} show strong seasonality in both humid and dry sites. In humid sites, production increased from a negligible amount in July (mid dry season) to a maximum of 0.04 ± 0.03 Mg C ha^{-1} mo^{-1} in November (early wet season), and decreased sharply over the following month. Assuming that the peak in flower litterfall captures a surge in NPP_{Flower} over the previous month [*Girardin et al.*, 2014], the peak in NPP_{Canopy} (dominated by leaf *NPP*) precedes the synchronised flowering event by two months. In dry sites, flowers were also produced in negligible amounts

thought the year, increasing significantly (p-value<0.0005) at the end of the dry season (September). The peak in flower production coincides with the peak in NPP_{Canopy} (Figure 3b).

Fruit - Annual estimates of fruit net primary productivity (NPP_{Fruit}) showed no significant difference between the two precipitation regimes (p-value = 0.20). The mean annual value for NPP_{Fruit} is 0.23 ± 0.007 Mg C ha^{-1} yr^{-1} (n = 8) for humid sites, and 0.18 ± 0.01 Mg C ha^{-1} yr^{-1} (n = 4) for dry sites.

We found a staggered fruiting phenology in both forest types. Assuming that the seasonality of fruit litterfall is a good proxy for the seasonality of NPP_{Fruit}, we observe a bimodal peak in fruit production in humid and dry sites. Values range from 0.03 ± 0.05 Mg C ha^{-1} yr^{-1} to 0.01 ± 0.01 Mg C ha^{-1} yr^{-1} in humid sites and from 0.03 ± 0.06 Mg C ha^{-1} yr^{-1} to 0.003 ± 0.004 ha^{-1} yr^{-1} in dry sites (Figure 3c). The seasonality of NPP_{Fruit} was surprisingly small at all sites.

3.2.3. Above-ground coarse woody net primary productivity

The mean annual value of above-ground coarse wood net primary productivity (NPP_{ACW}) is 2.08 ± 0.04 Mg C ha^{-1} yr^{-1} (n = 8) for humid sites, and 2.40 ± 0.09 Mg C ha^{-1} yr^{-1} (n = 4) for dry sites.

The seasonal trend of NPP_{ACW} is remarkably consistent between both precipitation regimes, with greater seasonal amplitude in dry sites. At all sites, wood production gradually increases from its lowest value in the dry season (June - August), to its highest value in the humid season (December - January). This gradual decline takes place over a period of 5 months. Then, NPP_{ACW} begins to decline before the end of the humid season (March), reaching values close to its lowest value as early as April. Values range from 0.23 ± 0.03 Mg C ha^{-1} yr^{-1} to 0.12 ± 0.04 Mg C ha^{-1} yr^{-1} (n = 8) in humid sites and from 0.38 ± 0.10 Mg C ha^{-1} yr^{-1} to 0.09 ± 0.03 Mg C ha^{-1} yr^{-1} (n = 4) in dry sites (Figure 2a).

3.2.4. Fine root net primary productivity

Mean annual values of fine root net primary productivity ($NPP_{\text{Fine roots}}$) differ significantly between humid and dry sites (p-value < 0.0005). The mean annual value for $NPP_{\text{Fine roots}}$ is 3.81 ± 0.08 Mg C ha^{-1} yr^{-1} (n = 8) for humid sites, and 2.24 ± 0.04 Mg C ha^{-1} yr^{-1} (n = 4) for dry sites.

$NPP_{\text{Fine rootss}}$ seasonality is remarkably low at all sites. We recorded a non-significant increase in root production at the start of the wet season in humid (p-value = 0.35), and dry sites (p-value = 0.15) (Figure 2, sup. mat. Figure S2).

3.3 Seasonal trends in *NPP* allocation

We explore the seasonal carbon allocation trends of each forest using ternary diagrams (Figures 4 and 5). A ternary diagram graphically depicts the ratios of the three variables as positions in an equilateral triangle. In figure 5, each of the three apexes of the triangle represent an NPP component, and each side represents a percent abundance scale. Each point plotted in the triangle represents the variance of monthly carbon allocation to NPP_{ACW}, NPP_{Canopy}, and $NPP_{\text{Fine roots}}$, as a percentage. It shows two distinct seasonal *NPP* allocation patterns. Dry sites (KEN-02, KEN-01, TAN-05, and TAN-06) have low variance in NPP_{Root} allocation, and high variance in NPP_{ACW} and NPP_{Canopy} allocation. This may suggest a constant allocation to fine roots, while there is a allocation trade-off between wood production and canopy production. Humid sites (CAX-03, CAX-06, CAX-08, TAM-05, and TAM-06) show little variance in allocation to NPP_{ACW}, but high variance in allocation between $NPP_{\text{Fine roots}}$ and NPP_{Canopy} (sup. mat. Figure S4).

The data used in Figure 5 are presented in the supplementary material as ternary diagrams of mean monthly *NPP* allocation for each plot (sup. mat. Figure S5). We interpret seasonal movements along an axis as an indication of a trade-off between two components. In the dry sites, we observe constant allocation to roots (e.g. ca. 30% allocation to $NPP_{\text{Fine roots}}$ throughout the year in KEN-01

and KEN-02), and a seasonal trade-off between NPP_{ACW} and NPP_{Canopy}. We find higher allocation to NPP_{ACW} during the wet season and higher allocation to NPP_{Canopy} during the dry season. In the humid sites, we observe constant allocation to NPP_{ACW} and a seasonal trade-off between $NPP_{Fine\ roots}$ and NPP_{Canopy}. We find higher allocation to $NPP_{Fine\ roots}$ during the wet season and higher allocation to NPP_{Canopy} during the dry season (sup. mat. Figure S5).

4. Discussion

4.1 Seasonal trends of net primary productivity

4.1.1. Leaf productivity

Discussions around the Amazon green up began with a series of optical remote sensing studies reporting a significant increase in greenness during the dry season [*Huete et al.*, 2006; *Myreni et al.*, 2007], which was interpreted as an increase in leaf production during the 2005 Amazonian drought [*Saleska et al.*, 2007; *Brando*, 2010]. Ecologically, this apparent enhanced leaf production was associated increased solar radiation, suggesting that Amazonian forests are light-limited rather than moisture-limited. The paradigm of light-limited forests was challenged by *Samanta et al.* [2010, 2012] and *Anderson et al.* [2010], who found no consistent impact of the 2005 drought on canopy productivity. *Morton et al.* [2014] went further by arguing that the Amazon dry season green up is an artefact of seasonal changes in near-infrared reflectance, an artefact of variations in sun-sensor geometry. When correcting for this artefact, these authors suggested no change in canopy production over an annual cycle. *Morton et al.* [2014] support the initial ground-based interpretations that seasonal moisture availability governs the balance between photosynthesis and autotrophic respiration in Amazonian forests [*Saleska et al.*, 2003, *Nepstad et al.*, 2002, *Phillips et al.*, 2009, *Meir and Woodward*, 2010]. *Restrepo Coupe et al.* [2013] and *Guan et al.* [2015]

suggest that Amazonian forests may be separated into radiation-controlled forests in wetter climates and precipitation-controlled forests in drier climates.

The field-based data presented here confirms that Amazon forests maximise leaf production during the dry season. At the plot level, our results support earlier interpretations that light-limited forests respond to an increase in daily insolation during the dry season [Borchert *et al.* 2014] (Figure 1a). We found that humid and dry sites show a peak in NPP_{Canopy} at the height of the dry season (August). One possible explanation is that these forests synchronise the timing of leaf production with the prospect of renewed water availability. Increased daily insolation may enhance radiation-limited photosynthesis as long as the system remains energy-limited rather than moisture-limited. This observation is consistent with *Wu et al.* [2015], who demonstrate that changes in leaf spectral characteristics with leaf age, with leaf flush occurring in the late dry season, drive the apparent green-up seasonal cycle in a site in Brazil.

Correlational evidence suggests that physical drivers control seasonal allocation patterns, results that are potentially valuable for Earth System Models. Leaf phenology of an old growth forest in steady state is likely to yield optimal carbon gain at the canopy level, so that trees adjust leaf gains and losses in response to environmental factors to achieve maximum carbon assimilation [*Caldararu et al., 2014*]. However, leaf production phenology is not a simple function of proximate cues such as radiation or precipitation, and should not be considered merely at the ecosystem level: the evolutionary perspective should be explored. A tropical forest is a collection of diverse species, and each canopy tree community consists of multiple species that compete with each other and might employ contrasting leafing phenology. Some may employ strategies to avoid competition with neighbouring trees, or exhibit seasonal leaf phenotypes to take advantage of seasonal windows of opportunity such as the early dry season, when solar radiation is high but the soil is still moist. Also, minimal insect activity, low fungal pathogen pressure and maximum

irradiance often co-occur in the dry season [*Lieberman*, 1982; *Aide*, 1988; *Givnish*, 1999]; hence the possibility that dry season leaf flush is an evolutionary response to minimise herbivory pressure on budding leaves must be considered [*Wright and Calderon*, 1995]. Avoidance of nutrient leaching during leaf expansion, when the leaf cuticle is not fully developed, has also been proposed as an evolutionary explanation [*Johnson et al. 2011*]. Further more, each individual within a species shares genes with its conspecifics but there is variation; gene expression adds another layer of complexity.

Reducing much of the complexity to light limitation vs. water limitation at the stand level is attractive. Nonetheless, we need to be aware that it may lead to incorrect models, and understanding intra- and interspecific competition and interactions between individuals would allow for a better understanding of community level leafing phenology.

Finally, edaphic factors are likely to affect a forest's seasonal trends: differences in precipitation regimes may depend on forest soils accumulating rainfall to generate enough subsurface water storage carried over for dry season plant water demand. Differences in soil physical properties (mainly soil depth) explains why the two plots at our Kenia site (dry site) display differing forest types, whilst experiencing identical climatic conditions and being only 1 km apart *Doughty et al.*, 2015].

4.1.2. Above-ground woody growth

An increase in NPP_{ACW} during the wet season, following a slow growth rate during the dry season is well established in the tropical ecological literature [*Wagner et al.*, 2012; *Rowland et al.*, 2013; *Doughty et al.*, 2014a]. Whereas the production of new leaves, flower and fruit may not deplete non-structural carbohydrate pools [*Wurth et al.*, 2005], wood production is likely to be carbon

limited [*Wagner et al.*, 2013]. Non-structural carbohydrate dynamics are involved in part of the stem growth and coarse root patterns, although understanding how they are involved requires further investigation (they were not measured in the current study). Understanding how non-structural carbohydrate dynamics are related to the seasonality of *NPP* components would further our understanding the response of tropical forests to seasonal changes in moisture availability [*Doughty et al.*, 2014a, *Doughty et al.*, 2014b]. Temporal buffering by non-structural carbohydrate reserves to enable a lag between photosynthetic seasonality and leaf, wood or root production may play an important role [*Doughty et al.*, 2014]. NSC may also be a pool that constrains our allocation results, not just as a buffer which can be drawn on: the possibility of active allocation to the NSC pool which also varies seasonally should be considered [*Hartmann et al.*, 2015].

4.1.3. Fine root productivity

On an annual timescale, humid sites produce more fine roots than dry sites, corroborating previous findings by *Metcalfe et al.* [2009] and *Girardin et al.* [2013]. On a seasonal timescale, fine roots show evidence of a response to an increase in moisture availability in humid sites. At those sites, the surge in root production at the start of the wet season coincides with an increase in NPP_{ACW}. One possible interpretation is an increase in allocation to roots to maximise the uptake of nutrients during a period of above-ground coarse wood growth.

We only report on fine root productivity for the top 0-30 cm depth. The present study investigates the seasonality of root growth and it is uncertain that total $NPP_{\text{Fine roots}}$ (including roots at a greater depth) would be comparable to that of roots from the top 0-30 cm depth. Studies from Amazonian forests indicate that the top 30 cm of soil contains 69 to 73% of total fine roots [*Jackson et al.*,

1998; *Quesada et al.*, 2011]. However, the importance of root growth in deep rooting moisture-limited forests requires further investigation [*Nepstad et al.*, 1994; *Metcalfe et al.*, 2009].

4.1.4. Fruit and flower production

We found minimal differences in the reproductive seasonality of forests across precipitation gradients. Flowering times affect plant success via the reproductive process. The timing and longevity of flower production dictates pollination rates and the subsequent timing and success of seed development, dispersal and germination [*Wright and Calderon*, 1995]. Hence, understanding the trends in flowering times is essential to understanding how plants will respond to changes in seasonal weather trends. However, the roles of biotic (e.g. competition for resources, pollinators and dispersers) and abiotic (e.g. weather) interactions in determining flowering phenology remain unclear.

The synchronised flowering observed at all our sites, including the wettest site with no distinct dry season, concurs with the phenological information gathered from Amazonia and Central America over the past decade [*Wright and van Shaik*, 1994; *Wright and Calderon*, 1995; *Brochert*, 2000; *Rivera*, 2002]. Our results support the hypothesis of increases in daily insolation as a cue for synchronised flowering [*Calle et al.*, 2009, 2010; *Brochert et al.*, 2005]. However, solar irradiance is unlikely to be a driver of NPP_{Flower}, rather a cue for an event governed by phylogeny [*Wright and Calderon*, 1995]. An intrinsic biological clock developed as an evolutionary response to biotic interactions may ultimately govern reproductive phenology. Humid sites experience a synchronised peak flowering episode in November. Dry sites experience a longer peak flowering season (September to November). An investigation of the seasonality of plant-herbivory and -pollination interactions in humid and dry sites may explain these trends. Many pollinators prefer dry conditions [*Frankie*, 1975], hence the dry season peak in flowering might be a response to an increase in pollinator activity, which in turn may be in synchrony with solar radiation and reduced

rainfall. The carbon allocated to flowering and fruiting is so small (< 10% of NPP) that seasonal changes in *NPP* are unlikely to be a driver of reproductive phenology.

We observe staggered fruitfall for both forest types, varying by species. Staggered phenologies are interpreted as an evolutionary response to reduce interspecific competition for pollinators and dispersers [*Foster et al.*, 1982; *Poulin*, 1999]. Staggered phenologies may also be interpreted as a strategy to optimise the success of seed germination. An increase in fruit fall at the beginning of the dry season allows drought tolerant plants to germinate in high solar irradiance. An increase in fruit fall at the end of the dry season allows moisture demanding plants to germinate in wetter conditions [*Chave et al.*, 2010].

As flowers and fruit have a short canopy lifetime, we assume that flower and fruit litterfall are a metric of their productivity rate, with a lag time of 1-3 mo for the fruiting. Hence, the values presented here are reported as NPP_{Fruit} and NPP_{Flower} [Girardin et al., 2014], with the important caveats that (1) frugivory may lead to a substantial underestimate of total fruit production and (2) fruit litterfall has a highly variable species-specific lag time of up to several months. Our data confirm that fruit litterfall has a highly variable lag time of up to several months, as reported by Mendoza et al. [2014]. However, why would plants spend big differences in time building fruits post pollination? Why don't we record evidence of staggered flowering to avoid competition for pollinators? The flowering and fruiting phenology of tropical forests remains a ripe area for future research.

4.2 Seasonal trends in *NPP* allocation

We identify two possible seasonal carbon allocation patterns (i) drier plots show evidence of constant allocation to roots and a seasonal trade-off between canopy and woody production; and (ii) humid plots show evidence of constant allocation to wood and a seasonal trade-off between roots and canopy production. None of our sites exhibited constant allocation to the canopy with a trade-off between roots and wood (Figure 5, Sup mat. Figure S5).

As our plots in this analysis are clustered into four sites, it is possible that spatial autocorrelation effects have an influence through edaphic factors or species composition effects, so caution is warranted before broadly assigning specific allocation strategies to specific precipitation regimes. Nonetheless, our observations are consistent with an interpretation that trees in water-limited sites increase water acquisition through fine roots, resulting in constant plot-level allocation to fine roots throughout the annual cycle. In contrast, trees in light-limited (humid) sites experience increased competition for light capture, resulting in constant plot level NPP allocation to woody growth. The vertical stratification in light resources in closed canopy forests may result in individual trees allocating *NPP* to stem growth over building new leaves to maximise light capture by the leaves it does have [*Wolf et al.*, 2011]. In both cases, inter-individual competition may be an important driver of *NPP* allocation, as predicted by game theory optimisation models. These models predict an increase in allocation towards the limiting resource beyond the collective optimum to deprive competitors of the limiting resource, resulting in non-optimal stand productivity [*Franklin et al.*, 2012]. Our results support this theory, as maintaining a high allocation to roots in systems where precipitation is a limiting factor and a high allocation to wood in irradiance limited systems may indicate competition for soil moisture and light, respectively.

All climate models predict a significant increase in temperatures and most predict an increase in seasonality [*Zelazowski et al*., 2010]. This will have immediate effects on water and light provision [*Urrutia and Vuille*, 2009; *Buytaert et al.*, 2011; *Solomon et al.*, 2009; *Arias et al.*, 2011]. Hence, understanding the process of resource allocation in humid and seasonally dry forests is an important step to improve our predictive understanding of the carbon cycle in a rapidly changing climate. Existing models are especially weak on their use of allocation coefficients, often applying coefficients to all broadleaf tropical evergreen forests. However, our results demonstrate important variations in allocation coefficients between seasons and between wet and dry sites. The information collected by the GEM protocol may be used in models to explore direct responses to light and moisture availability on an interannual scale: Does allocation strategy change in dry years or is it a fixed property of the trees in a forest stand? Does a decline in tree growth during drought reflect reduced productivity or merely a shift in allocation strategy? Do moisture availability thresholds control these trends (i.e. how much dryer would a dry site have to get before these patterns change)? Are wet or dry sites more sensitive to changes in precipitation? The insights provided in our study are important in addressing questions on forest response to drought, and how that response may vary across the Amazon basin.

5. Conclusions

The ground-based data described in the present study indicates that the Amazon forests we studied maximise leaf production during the dry season. This implies that an increase in solar irradiance during the dry season leads to an increase in photosynthesis in forests where radiation and fresh leaf area are limiting factors. As for reproductive trends, NPP_{Flower} seasonality appears to be synchronised with the seasonality of solar irradiance. However, solar irradiance may not be a driver of NPP_{Flower}, rather a cue for an event governed by phylogeny.

We identify two main seasonal allocation strategies: trade-offs between allocation to wood and canopy (dry sites), and trade-offs between allocation to roots and canopy (humid sites). Understanding the processes that govern seasonal carbon allocation strategies of humid and dry forests will help us understand their phenological responses to a transition from radiation-limited to moisture-limited forests. The correlational evidence for present day forests suggests dominant roles for precipitation and radiation controls over seasonal allocation patterns. However, it is still possible that those allocation patterns emerged from the data for other reasons (e.g. herbivore pressure, pollinator incidence) and further research is needed to understand the ecological and evolutionary mechanisms that control seasonal allocation patterns.

Phenological models for tropical forest ecosystems remain poorly developed [*Morin and Chuine*, 2005; *Sakai*, 2001]. To understand the seasonal trends of tropical forest productivity, we must begin by explaining the complex interactions between plant physiology, abiotic and biotic factors, and evolutionary biology. One of the main limitations of representing tropical forests in Earth System Models is our incomplete understanding of the allocation strategies of different forests (REF needed). Systematic collection of the same metrics of *NPP* across multiple sites allows for new insights on seasonal, annual and inter-annual allocation strategies of tropical forests. We hope that our present attempt to decipher the seasonal trends of *NPP* allocation in lowland Amazonia will help the research community towards improvements in the predictive power of these models.

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Table 1

	Western Amazonia Transect						Eastern Amazonia				
RAINFOR site code	ALP-11	ALP-30	TAM-05	TAM-06	KEN-01	KEN-02	CAX-04	CAX-06	CAX-08	TAN-06	TAN-05
Latitude	-3.95	-3.9543	-12.8309	-12.8385	-16.0158	-16.0158	-1.7160	-1.7369	-1.7160	-13.0765	-13.0765
Longitude	-73.4333	-73.4267	-69.2705	-69.296	-62.7301	-62.7301	-51.4570	-51.46194	-51.4570	52.3858	52.3858
Elevation (m asl)	120	150	223	215	384	384	47	47	47	385	385
Solar radiation (GJ m^{-2} yr^{-1})	5.2		4.8		5.9			5.7		6.74	
Mean annual air temperature (°C)	25.2		24.4		23.4			25.8		25	
Precipitation (mm yr^{-1})	2689		1900		1310			2311		1770	
Mean MCWD (mm)	-6		-259		-386			-203		-482	
Soil moisture (%)	26.8 ± 0.3	10.8 ± 0.2	21.8 ± 0.2	35.5 ± 0.4	19.7 ± 0.4	16.0 ± 0.3	22.4 ± 0.1	27.1 ± 0.3	22.4 ± 0.1	10.7 ± 0.2	10.8 ± 0.2
Soil type	Alisol/Gleysol	Arenosol	Cambisol	Alisol	Cambisol	Cambisol	Vetic Acrisol	Ferralsol	Terra Preta	Ferralsol	Ferralsol
P_{total} (mg kg^{-1})	125.6	37.6	256.3	528.8	447.1	244.7	37.4	178.5	37.4	147	147
Total N (%)	0.1	0.08	0.16	0.17	0.22	0.17	0.06	0.13	0.06	0.16	0.16
Total C (%)	1.19	1.13	1.51	1.2	2.4	2	0.83	1.68	0.83	2.55	2.55
Soil C stock (Mg C ha^{-1} from 0-30 cm)	92.95	16.4	43.7	37.4	74.8	67.1	35	51.9	35	67.1	67.1
Soil organic layer depth (cm)	12	10	13	37	32	54	30	35	30	28	28
Cation exchange capacity ($mmol_c$ kg^{-1})	30.4	4.9	44.8	56.8	75.58	60.74	1.34	22.82	1.34	19.47	19.47
Sand (%)	65	82	40	2	58.05	55.48	83.69	32.54	83.69	45.73	45.73
Clay (%)	15	2	44	46	19.13	18.25	10.68	53.76	10.68	48.9	48.9
Silt (%)	20	16	17	52	22.82	26.27	5.64	13.7	5.64	5.37	5.37

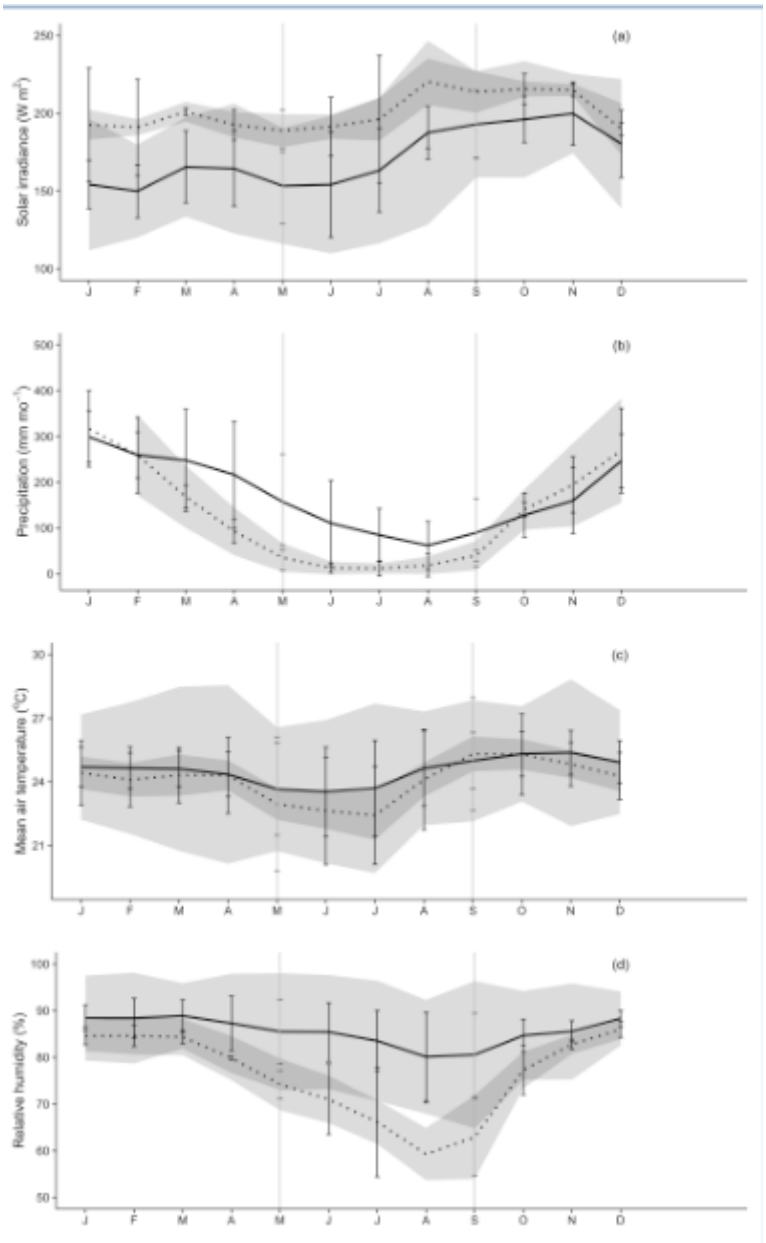

Figure 1. Seasonality of weather variables in three lowland Amazonian forests sites in Peru, Bolivia and Brazil. Weather stations were located at Tambopata (TAM-05), Kenya (KEN-01), Caxiuanã (CAX-06), Allpahuayo (ALP-01) and Tanguro (TAN-05), and Solar irradiance (W m^{-2}), precipitation (mm mo^{-1}), air temperature (ºC) and relative humidity (%) are presented on a monthly timescale, as a mean over three years (2009-2011). Solid lines represent the average of humid sites (Caxiuanã, Tambopata, Allpahuayo) and dotted lines represents the dry sites (Kenya, Tanguro). The KEN-01 weather station is used in both dry and humid site analysis, as it is the local weather station for KEN-01 and KEN-02. Interannual variability are provided as grey ribbon (± SD), intersite variability are presented as error bars centred on the mean, (± SD).

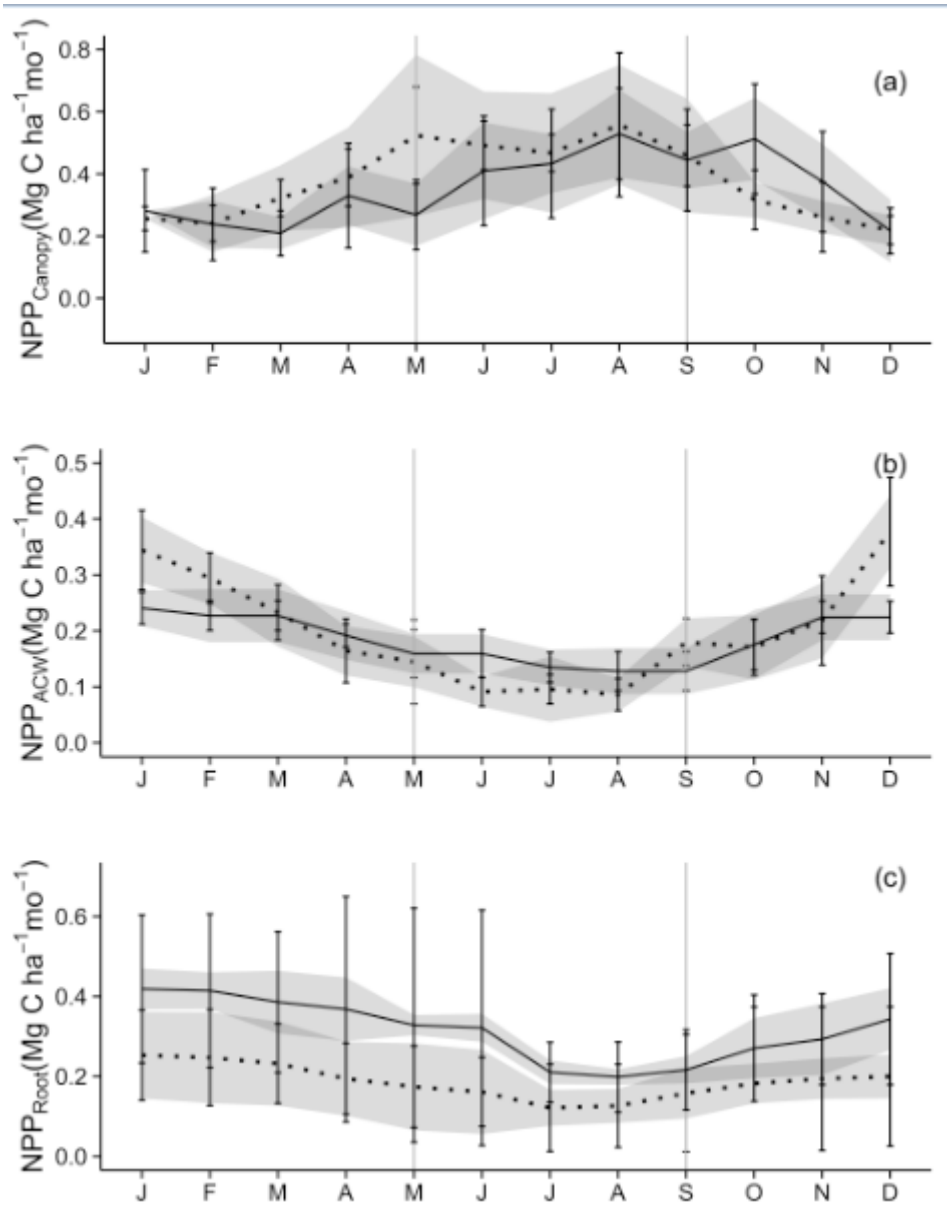

Figure 2. Seasonality of net primary productivity components in ten lowland Amazonian forest plots in Peru, Bolivia and Brazil. Data were averaged over humid sites (solid line, ALP-01, ALP-30, CAX-03, CAX-06, CAX-08, TAM-05, and TAM-06), and dry sites (dotted line, KEN-02, KEN-01, TAN-05, and TAN-06). Net primary productivity of leaf (NPP_{Leaf}), above-ground coarse wood (NPP_{ACW}) and fine roots ($NPP_{Fine\ roots}$) are presented on a monthly timescale, as a mean over three (2009-2011) or four (2009-2012, Tambopata) years. The start and end of the dry season is represented by vertical grey lines. Interannual variability are provided as grey ribbon (± SD), intersite variability are presented as error bars centred on the mean, (± SD). Data for each plot are provided in Supplementary Material.

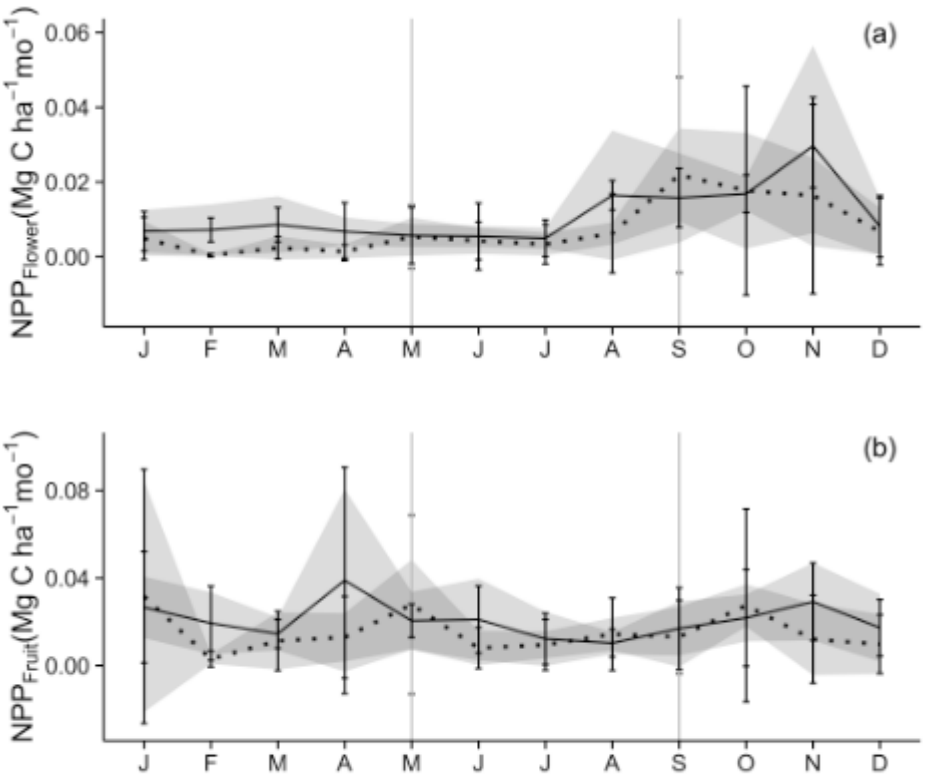

Figure 3. Seasonality of net primary productivity of reproductive organs in nine lowland Amazonian forest plots, Peru, Bolivia and Brazil. Data were averaged over humid sites (solid line, ALP-01, ALP-30, CAX-03, CAX-06, CAX-08, TAM-05, and TAM-06), and dry sites (dotted line, KEN-02, KEN-01, TAN-05, and TAN-06). Net primary productivity of flower (NPP_{Flower}), and fruit (NPP_{Fruit}) are presented on a monthly timescale, as a mean over three (2009-2011) or four (2009-2012, Tambopata) years. The start and end of the dry season is represented by vertical grey lines. Interannual variability are provided as grey ribbon (± SD), intersite variability are presented as error bars centred on the mean, (± SD). Data for each plot are provided in Supplementary Material.

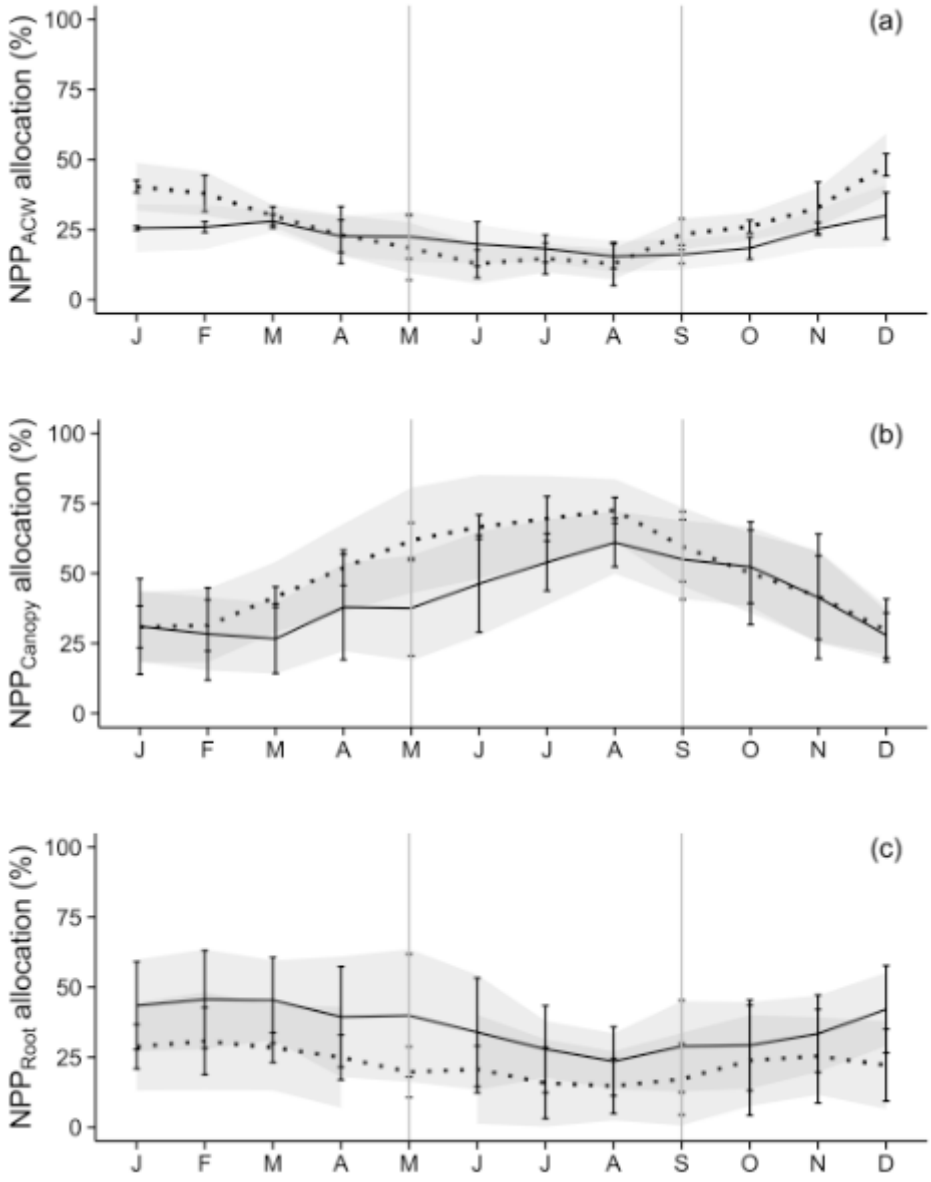

Figure 4. Seasonality of net primary productivity allocation to canopy (NPP_{Canopy}), above-ground coarse wood (NPP_{ACW}) and fine roots ($NPP_{Fine\ roots}$) in nine lowland Amazonian forest plots, Peru, Bolivia and Brazil. Data were averaged over humid sites (solid line, ALP-01, ALP-30, CAX-03, CAX-06, CAX-08, TAM-05, and TAM-06), and dry sites (dotted line, KEN-02, KEN-01, TAN-05, and TAN-06). Allocation data are presented as percentage of total *NPP* allocated to each component each month, as a mean over three (2009-2011) or four (2009-2012, Tambopata) years. Interannual variability are provided as grey ribbon (± SD), intersite variability are presented as error bars centred on the mean, (± SD). Data for each plot are provided in Supplementary Material.

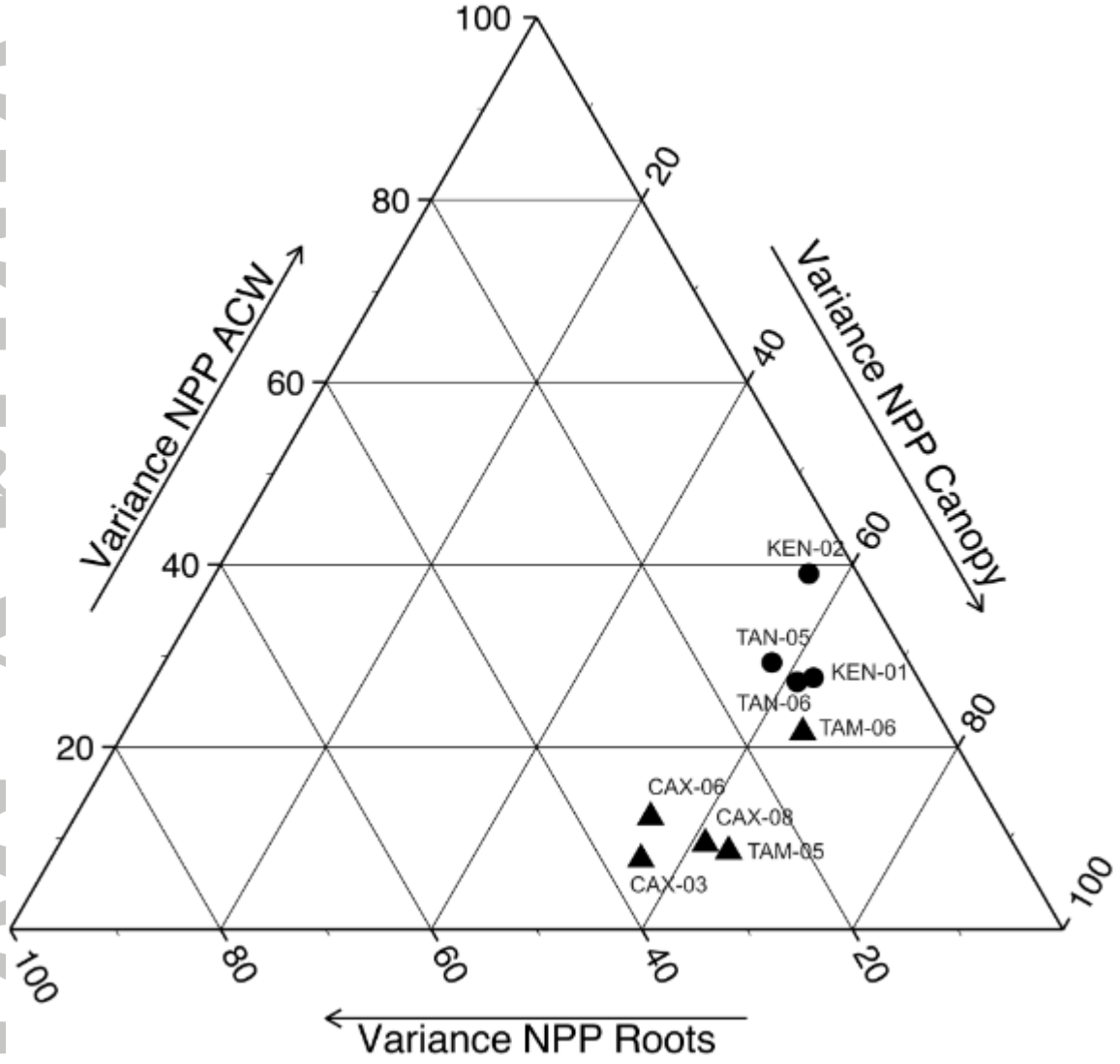

Figure 5. Ternary diagram of the normalised variance of seasonal allocation of net primary productivity in eight lowland Amazonian forest plots, Peru, Bolivia and Brazil. Normalised variance was calculated as the variance of each component divided by the sum of the variances (NPP_{Leaf}, NPP_{ACW}, and $NPP_{Fine\ roots}$). Each point represents the annual variance of *NPP* allocated to components, as a mean over three (2009-2011) or four (2009-2012, Tambopata) years. Data were averaged over humid sites (solid line, CAX-03, CAX-06, CAX-08, TAM-05, and TAM-06), and dry sites (dotted line, KEN-01, KEN-02, TAN-05, and TAN-06). We did not have sufficient data from Allpahuayo to carry out this analysis. Circles represent dry sites, triangles represent humid sites.